Check for updates

Received: 28 August 2023 | Revised: 31 May 2024 | Accepted: 11 June 2024

DOI: 10.1111/geb.13883

Global Ecology and Biogeography | A Journal of Macroecology

WILEY

RESEARCH ARTICLE

# Salinity plays a limited role in determining rates of size evolution in fishes globally across multiple scales

John T. Clarke[1,2,3,4,5,6] | Robert B. Davis[5]

[1]GeoBio-Center, Ludwig-Maximilians-Universität München, Munich, Germany

[2]Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, Munich, Germany

[3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[4]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

[5]Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[6]Department of Ecology and Biogeography, Faculty of Biological and Veterinary Sciences, Nicolaus Copernicus University, Toruń, Poland

**Correspondence**
John T. Clarke, GeoBio-Center, Ludwig-Maximilians-Universität München, Munich, Germany.
Email: j.clarke.paleo@gmail.com

**Funding information**
Alexander von Humboldt-Stiftung; Eesti Teadusagentuur, Grant/Award Number: PRG741; Deutsches Zentrum für integrative Biodiversitätsforschung Halle-Jena-Leipzig, Grant/Award Number: DFG-FZT 118, 202548816; Polish National Agency for Academic Exchange, Grant/Award Number: NAWA PPN/ULM/2019/1/00248/U/00001

**Handling Editor:** Kevin Healy

## Abstract

**Aim:** Substantial progress has been made to map biodiversity and its drivers across the planet at multiple scales, yet studies that quantify the evolutionary processes that underpin this biodiversity, and test their drivers at multiple scales, are comparatively rare. Studying most fish species, we quantify rates of body size evolution to test the role of fundamental salinity habitats in shaping rates of evolution at multiple scales. We also determine how four additional factors shape evolutionary rates.

**Location:** Global.

**Time Period:** Extant species.

**Major Taxa Studied:** Actinopterygii.

**Methods:** In up to 1710 comparisons studying over 27,000 species, we compare rates of body size evolution among five salinity habits using 13 metrics. The comparisons span a molecular tree, 100 supertrees, and 10 scales of observation to test for robust patterns and reveal how patterns change with scale. Then, three approaches assess the role of three non-salinity factors on rates, and an alternative habitat scheme tests if lakes influence evolutionary rates.

**Results:** Rates of size evolution rarely differ consistently between salinity habitats; rate patterns are highly clade- and scale dependent. One exception is freshwater-brackish fishes, which possess among the highest size rates of any salinity, showing higher rates than euryhaline fishes in most groupings studied at most scales, and versus marine, freshwater and marine–brackish habitats at numerous scales. Additionally, species richness had the greatest potential to predict phenotypic rates, followed by branch duration, then absolute values of body size. Lacustrine environments were consistently associated with high rates of size evolution.

**Main Conclusions:** We reveal the rate patterns that underpin global body size diversity for fishes, identifying factors that play a limited role in shaping rates of size evolution, such as salinity, and those such as species richness, age and lake environments that consistently shape evolutionary rates across half of vertebrate diversity.

KEYWORDS
body size evolution, brackish, fish evolution, freshwater, marine, phenotypic rates

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

## 1 | INTRODUCTION

Understanding the mechanisms driving biodiversity on the planet, including how and why these mechanisms vary with scale, is crucial for evolutionary biology and macroecology. Substantial progress has been made to recognize (Blackburn & Gaston, 2002) and document (Clarke, 2021; Finlay et al., 2006; Foody, 2004; McClain & Nekola, 2008; Rahbek, 2005) patterns and drivers of present-day biodiversity at multiple scales. By contrast, similarly broad efforts to understand what factors drive differences in the evolutionary processes that underlie this biodiversity (e.g. rates of phenotypic evolution), and how these vary with scale, are comparably rare, despite their ability to deliver significant insights. For example, while a positive relationship between speciation rates and rates of size evolution exists at the global scale, it is frequently weak or absent at lower taxonomic scales (Cooney & Thomas, 2020). Additionally, different functional traits can differ in the taxonomic scale at which they show their highest rates of evolution; for example, jaw traits may show higher rates at higher taxonomic scales, while higher rates of body size evolution may occur at lower taxonomic scales (Slater & Friscia, 2019). Fishes, comprising over half of vertebrate diversity (34,000+ species) and varying over three orders of magnitude in body length, possess huge potential to deliver highly generalizable results regarding how ecological conditions shape evolutionary processes at multiple scales, and specifically here, rates of phenotypic evolution (i.e. the amount of variance accumulated per million years along branches of a phylogeny). Furthermore, fishes are uniquely positioned to test drivers of evolutionary mechanisms in lesser-studied aquatic systems, as they occupy nearly every aquatic environment.

One of the most fundamental factors thought to shape biodiversity and its underlying evolutionary processes in aquatic ecosystems is the divide between marine and freshwater environments, and numerous hypotheses exist for why evolutionary rates may differ between them. Darwin described how freshwater conditions promote slow evolutionary processes, due to reduced competition and smaller population sizes relative to marine environments (Darwin, 1859, 1877; Darwin & Seward, 1903). In contrast, most contemporary research emphasizes mechanisms in freshwater habitats, primarily habitat fragmentation, which are expected to drive elevated diversification and phenotypic rates through reproductive isolation, local adaptation and smaller population sizes (Puebla, 2009; Seehausen & Wagner, 2014; Tedesco et al., 2017). Fragmentation involves two key components of adaptive radiation theory (Losos, 2010; Schluter, 2000; Simpson, 1953): (1) the generation of novel habitats (i.e. new rivers and lakes) harbouring ecological opportunity, and (2) transition events, as species colonize these new habitats. Although it has been suggested that a higher number of transitions into freshwater from marine habitats promotes elevated evolution in the former relative to the latter (e.g. Mitterboeck et al., 2016), when all salinity habitats are considered, marine and freshwater habitats receive similar numbers of lineages from other habitats (Clarke, 2021); this implies that the higher number of internal "within freshwater" transitions (i.e. into new rivers and lakes) specifically deserves more focus than transitions into freshwater alone.

Testing expected differences in evolutionary process by salinity, both broadly and at multiple scales, is challenging, owing to the rarity of organisms that cross the marine–freshwater divide (Lee & Bell, 1999). Fishes present an exception, as many lineages transition between these environments. This repeatability provides an ideal "natural experiment" to elucidate whether salinity habitat influences rates of size evolution. Furthermore, substantial work on how salinity influences evolution has focused on fishes, such as Darwin's theories on slow freshwater evolution. In contrast, broad-scale work has highlighted similarities in the major axes of morphological evolution explored by marine and freshwater fishes, potentially due to shared evolutionary opportunities across the depth gradient in both environments (Friedman et al., 2022), which may imply similar evolutionary rates. Friedman et al. (2022) also revealed important differences, including (1) the greater spread of marine fish morphologies, which may imply higher marine rates, and (2) that while marine clades generally occupy distinct regions of morphospace (high phylogenetic signal), freshwater clades have repeatedly evolved similar morphologies to each other (low phylogenetic signal), which may imply higher rates in freshwater taxa if this "re-evolution" more reliably delivers higher rates than an average marine clade evolving within confined and distinct regions of morphospace. It is possible both of these seemingly conflicting rate expectations hold true, but at different scales, with higher freshwater rates at lower taxonomic scales, and higher marine rates in a full dataset analysis. Thus, a multi-scale test could reveal how evolutionary rates differ by scale.

Fishes also permit refined tests for the impacts of salinity habitat on evolution beyond a binary focus on marine and freshwater. Fishes can be assigned to at least five salinity habitats by also considering freshwater–brackish, marine–brackish and euryhaline lifestyles. Rate expectations for all five salinity habitats can be derived from a recent finding that mean fish body size varies systematically between these salinity habitats across all phylogenetic scales; freshwater taxa are on average the smallest, freshwater–brackish and marine taxa are medium sized and euryhaline and marine–brackish taxa are the largest (Clarke, 2021). We can derive evolutionary rate expectations from these size differences, because we expect a negative association between body size and evolutionary rates due to the high species richness of small species globally, implying small taxa possess high speciation rates. We also expect higher speciation rates in small species to co-occur with higher rates of size evolution, as there is widespread evidence for this correlation in vertebrates (Cooney & Thomas, 2020). Thus, observed average size differences among salinity habitats would suggest that evolutionary rates are highest in smaller freshwater fishes, are intermediate in freshwater-brackish and marine fishes and are lowest in larger-sized euryhaline and marine–brackish fishes.

While progress has been made testing the role of salinity habitat on fish speciation rates at broad scales. (Miller, 2021; Rabosky, 2020), for phenotype, broad-scale studies focus specifically on phenotypic differences (Clarke, 2021; Friedman et al., 2022), meaning that phenotypic rate comparisons are mostly derived from clade-specific case studies that often report conflicting results (Betancur-R et al., 2012; Davis et al., 2014; Guinot & Cavin, 2018; Kolmann et al., 2020; Santini

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

et al., 2013; Thacker, 2014). Thus, it is difficult to ascertain whether these conflicting results accurately reflect reality or occur due to differences in methods and phylogenetic scale. Our aim, using both an ~11,000-species molecular tree and one hundred ~27,000-species supertree datasets of body size and salinity habitat for actinopterygian fishes, is to test whether rates of size evolution differ between salinity habitats when examined across 10 phylogenetic scales. This allows us to overcome ascertainment bias and reveal the overall architecture of rate patterns, showing how these rates differ within and between scales, and determining whether results for the whole phylogeny are underpinned by consistent outcomes at lower scales. We used both a phylogeny that only includes taxa with molecular data, and supertrees that add the rest of fish diversity using taxonomic data, to help us evaluate whether a recently demonstrated size bias in the molecular taxon sample towards larger absolute body sizes (Clarke, 2021) has a discernible impact upon rates of size evolution. In addition, we use up to 1056 comparisons and the full dataset to evaluate the role of three additional variables on rates of size evolution. Finally, we examine an alternative aquatic habitat scheme to explore how lakes and rivers impact rates of phenotypic evolution.

We designed the study to overcome ascertainment bias, where clades that are more varied in the predictor variable of interest (e.g. number of salinity habitats occupied) are more likely to be studied. This is important, as "hotspot" clades for salinity variation in fishes (i.e. clades that explore many salinity habitats) are more likely to show atypical patterns of absolute size differences than non-hotspot clades (SI text of Clarke, 2021). To avoid this bias, and to achieve additional benefits outlined in the introduction, we test for rate differences within all definable groups across 10 different phylogenetic scales. Phylogenetic scales 1–7 test patterns at increasingly broad phylogenetic scales, first testing all families (1), orders (2), then successively larger groupings on the phylogeny termed Tax3, Tax4, Tax5 and Tax6 (where the phylogeny is split into 13, 9, 5 and 3 sections respectively), followed by the full dataset (7). The final three scales (8–10) have a different goal, targeting groupings considered "evolutionary hotspots" for salinity to test for ascertainment bias (8), then expanded versions of these hotspots to assess whether inclusion of species surrounding phylogenetic hotspots has a mediating effect (9), and order-level groups with hotspot orders removed (10) to exclusively consider non-hotspot clades.

## 2 | MATERIALS AND METHODS

### 2.1 | Data, phylogenetic scales for comparisons and molecular versus supertree analyses

We conducted our analyses using an 11,638-tip molecular tree of actinopterygians and its associated 100 supertrees (Rabosky et al., 2018), referred to as the 11k tree and 31k trees herein. Actinopterygian species in FishBase (Froese & Pauly, 2000) are coded as absent/present in brackish, marine and freshwater habitats. These were assigned to six salinity lifestyles to capture each unique combination of states, depending on whether taxa were coded as: exclusively (1) marine, (2) freshwater or (3) brackish, both freshwater and brackish (4. freshwater–brackish), both marine and brackish (5. marine-brackish), both marine and freshwater (6. euryhaline). Thus, species were assigned to the most specific and representative categories possible with this data, making the fewest possible assumptions (i.e. not forcing groups together), while allowing direct comparisons to previous work that recovered clear absolute body size differences between these specific habitats (Clarke, 2021). We extracted all actinopterygian fishes with maximum body size (in cm) listed in FishBase; the metric most widely used in other macroevolutionary analyses of fishes (e.g. Rabosky et al., 2013). Two datasets were constructed: a 10,906-species dataset with both size and salinity data for taxa in the 11k tree, and a 27,226-species dataset with both size and salinity data for taxa in the 31k tree. Analyses were run on both 11k- and 31k-tree matched datasets. Both dataset types have potential biases, as body sizes are biased towards larger size in molecular-tree sampled taxa (Clarke, 2021), while some types of supertrees may also alter phenotypic rate results (Rabosky, 2015); thus, it is important to consider both.

### 2.2 | Testing for differences in size rates between salinity habitats

Pairwise rate comparisons were made among five of our six salinity habitats (e.g. freshwater versus marine). The sixth habitat, which consisted of exclusively brackish taxa, was excluded because it contains too few species to perform repeated comparisons with other salinity habitats. More specifically, comparisons are made between these habitats for each grouping (i.e. within the 10 scales described above). For example, at the family scale, each family represents a grouping. A hypothetical fish family containing marine, freshwater, freshwater-brackish, and euryhaline taxa would, therefore, permit six unique pairwise comparisons between these habitats. Thus, the number of pairwise salinity comparisons made within all groupings studied (i.e. considering all groupings at all scales) totals 1056 and 1710 for the 11k-tree and 31k-tree datasets respectively. For every comparison, 13 metrics are used to compare rates of size evolution. The first five of these metrics pertain to those obtained from non-log-transformed BAMM tip-rate data. BAMM uses a Bayesian framework to estimate shifts in rates of trait evolution across a phylogeny within a Brownian motion framework (Rabosky et al., 2014). Convergence was achieved for the 11k-tree run for 1 billion generations, sampling every 380,000 generations, with the first 15% of samples as burn-in. To achieve convergence on the 31k supertree, the tree was split into six segments, and each was run for 1.5 billion generations, sampling every 375,000 generations, and segments merged using the "add_subclade_to_backbone_BAMM" function (Igea et al., 2017). Priors were derived from the SetBAMMPRIOR function, and convergence was checked with CODA (Plummer et al., 2006). The five metrics derived from BAMM rates are: (1) mean BAMM tip rates, and the use of these tip rates to compute the following four metrics; (2) a Wilcoxon

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

test, employed as a check for potential to recover differences as a function of non-phylogenetically corrected rate and sample size; (3) simulation phylogenetic ANOVA significance tests in R package phytools (Revell, 2012), widely used in the literature, permitting direct comparisons between our results and other studies; (4) phylogenetic mean rates, derived from phylogenetic "correction" from PGLS ANOVA in R package RRPP (Collyer & Adams, 2018), which presents an advantage over simulation ANOVA as its parameter estimates are explicitly conditioned upon the phylogeny; and (5) RRPP ANOVA's associated significance test. The same five metrics were then obtained for log10 mean BAMM tip rates (metrics 6–10). The compare.rates function in R package geomorph (Adams & Otárola-Castillo, 2013) and its associated statistical test (metrics 11–12) provide an alternative test of evolutionary rates to BAMM. compare.rates estimates the Brownian motion rate parameter for each comparison group (e.g. freshwater vs. marine pufferfishes) and compares the ratio of these values relative to simulations. compare.rates is applied once for every comparison in the 11k-tree dataset, and then over the 100 topologies of the 31k-tree datasets (except for the largest phylogenetic scales, which are run once due to computational demands). Metric 13 is STRAPP's significance test in BAMMtools (Rabosky & Huang, 2016). It provides a highly conservative correction of rates relative to PGLS by downweighing species within the same rate regime. Additional corrections for multiple comparisons are not made to each individual metric because our study does not overinterpret individual significant results from a specific metric, but looks for consistent trends across metrics to inform conclusions. Together, these thousands of results allow the reader to examine any specific metric or clade comparison of interest (Supplementary Appendices 1–4) and allow us to test for robust patterns that hold across datasets and scales. BAMM runs, together with other rate comparisons, took several months to compute.

### 2.3 | Testing alternative drivers of rate variation

Beyond salinity habitat, we tested three alternative predictors of rate (species richness, tip-branch duration, and absolute size) with three approaches (A–C in Table 1), allowing us to examine both variables assigned to groups (e.g. species richness) and those assigned to species (e.g. body size). Considering results from all three approaches, associations are ranked by their degree of support (Table 1). Approaches A and B required defining groups of taxa for comparison. For this, we used the 125 unique pairwise salinity habitat comparisons derived from our order-scale groupings in the 11k-datasets (i.e. comparisons that constitute the Ord. column of Figure 2a).

Approach A (Table 1A) assessed whether each theorized association in Table 1 is plausibly active (yes/no) in each of the 125 comparisons (Supplementary Appendix 5). For example, to test support for the hypothesized negative association between rates of size evolution and branch duration in just one comparison (e.g. between marine and freshwater pufferfishes), one determines whether the habitat with the shorter mean tip-branch durations also possesses the higher mean rate of size evolution. If true, this single comparison supported the negative association between branch duration and size evolution rate. We then calculated what percentage of comparisons supported the association, and because these 125 comparisons are a mixture of all 10 sets of pairwise habitat comparisons (e.g. all marine vs. freshwater order comparisons represent one set), we also obtained percentage support within each of the 10 sets (Supplementary Appendix 6) to reveal if specific associations are prevalent for specific environmental comparisons (e.g. if shorter branch durations only correlate with higher size rates in marine vs. freshwater comparisons). Notably high/low percentages are presented in Table 1A.

Approach B tested the three associations in a continuous manner to determine the extent to which increases in one variable (when comparing between two habitats) are met by corresponding increases/decreases in the second variable; this determines the strength of each association. For each variable, a regression was performed for each of the 10 pairwise habitat comparisons (i.e. all order-level comparisons between marine and freshwater habitats comprise one regression) to determine if the relationship changes depending upon the habitats compared (Supplementary Appendices 7–9, summarized in Supplementary Appendix 10). Table 1B displays information on whether a majority of the 10 regressions were positive or negative, and the average $R^2$ and $p$ values for whichever sign formed the majority (e.g. average of all positive associations). Approach C tests for an association between rates of size evolution and absolute body size with the full dataset using STRAPP (only applicable to species-specific variables).

Finally, we tested whether lacustrine species exhibited higher rates of body size evolution (Supplementary Appendices 11 and 12) using the scheme applied by Miller (2021). Analysis data are provided in Supplementary Appendices 13–18.

## 3 | RESULTS

### 3.1 | Rates of size evolution between salinity habitats

11k-tree full-dataset log size rate distributions show minor differences between habitats (Figure 1a); only median rates for freshwater–brackish taxa appear notably higher than median rates for other salinities. No phylogenetic statistical tests, applied to untransformed or logged full-dataset BAMM rates for the 11k dataset, recover significant differences between any two habitats, yet one does emerge with the 31k-tree dataset (Figure 1b): higher rates in freshwater–brackish taxa versus marine–brackish taxa ($p = 0.007$, compare.rates; Supplementary Appendix 3). Phenotypic rates in the 31k-tree dataset are inflated relative to the 11k-tree dataset in every habitat (Figure 1).

Rate differences between habitats were assessed for each unique pairwise habitat comparison (e.g. marine vs. freshwater) by (1) calculating the percentage of clades where mean rate in one habitat is larger than the other within each phylogenetic scale (e.g. when comparing marine and freshwater rates at the family scale, one considers only those families containing both marine and freshwater species,

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

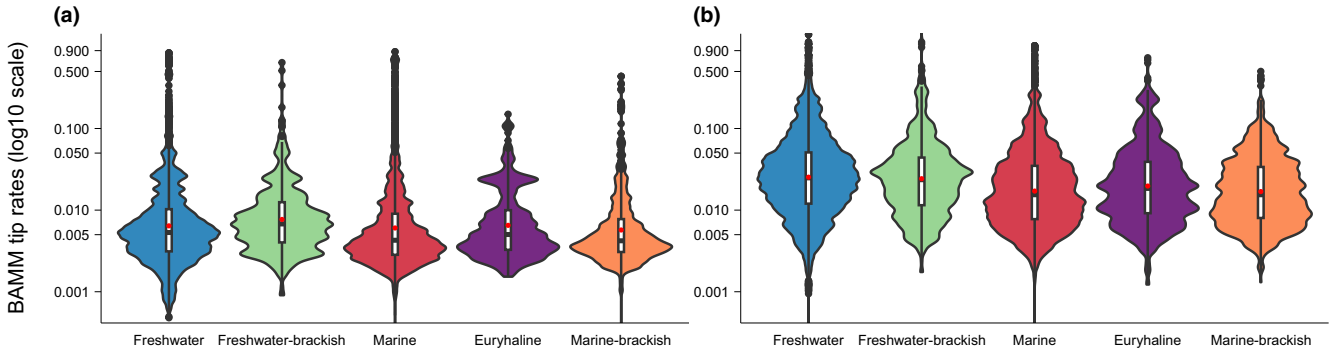


**FIGURE 1** Distributions of phenotypic log10 tip rates for taxa in each salinity habitat using (a) the 11k-tree dataset and (b) the 31k-tree dataset. Tip rates represent the Brownian rate parameter with units of $\log(cm)^2/myr$.

and asks in what percentage of the families the marine species possess higher mean rates); and (2) assessing whether patterns regarding these percentages remain consistent across multiple phylogenetic scales. Thus, if there were a highly consistent pattern of rate difference between any two habitats (i.e. where most clades at most scales tended to show higher rates in one habitat relative to another), we expect the individual rows of Figure 2a to be dominated by a single colour. However, rows are rarely dominated by a single colour, illustrating a lack of consistency regarding which habitats possess higher rates than others; rate patterns vary considerably with clade and scale. Only one finding—higher rates in freshwater-brackish taxa versus euryhaline taxa—consistently emerges in a majority of examined clades at most scales (i.e. occurring in over 50% of comparisons within each scale, but most commonly for 70%–100% of comparisons). This result emerges at all but one phylogenetic scale using both the 11k- and 31k-tree datasets (Figure 2a–c, row 3). This finding is maintained regardless of which mean rate metric (untransformed tip rate, log10 tip rate, PGLS tip rate and compare.rates means) is used to compare rates of size evolution (see row 3 in the following figures: Figure 2, pages 2, 4, 10 and 12 of Supplementary Appendix 1, page 2 of Supplementary Appendix 2). However, even for this strongest result, this finding does not emerge for evolutionary hotspot comparisons, where either exactly 50% of the groupings examined show higher freshwater–brackish rates relative to euryhaline rates (Figure 2a,b, row 3) or even less than 50% (compare.rates function, see row 3 of pages 2, 4, 10 and 13 of Supplementary Appendix 1 and page 2 of Supplementary Appendix 2). This shows the potential for "evolutionary hotspot" clades (i.e. that explore many salinities) to show atypical patterns relative to non-hotspot clades, as has been seen for body size patterns (Clarke, 2021). The results of every rate comparison made in the study, with each of our metrics (including each test for statistically significant differences), are available in Supplementary Appendices 1–4.

## 3.2 | Alternative drivers of size rates

Table 1 summarizes the degree of support recovered for three theorized rate drivers from three distinct approaches. Together, these inform a relative ranking, from the strongest (1) to the weakest (3), as listed in Table 1 alongside a support statement. Thus, phenotypic rates are best correlated with species richness, followed by branch duration, then absolute body size. As an illustrative example, we here interpret the results for the association ranked 1st—the hypothesized (yet rejected) positive association between phenotypic rates and species richness (Table 1).

Method A shows that only in a minority of comparisons (38.4% of the 125 order-level comparisons), the group with higher species richness also shows higher rates of phenotypic evolution (Supplementary Appendices 5 and 6). Table 1A reports noteworthy results, showing this percentage can fall as low as 20% when examining the 12 freshwater versus marine–brackish comparisons or the 18 euryhaline versus marine–brackish comparisons. Beyond reading Supplementary Appendices 5 and 6, one can visually assess which individual within-order habitat comparisons show a positive or negative association between rates and species richness in Supplementary Appendix 7. Each of the 10 plots depicts contrasts in richness and rates between two specific habitats; points in grey quadrants support a negative association while points in white quadrants support a positive association. These 10 contrast plots form the basis of the 10 regressions that define method B. As for method A, the hypothesized positive association is rejected, as only 2 of the 10 regressions find any positive relationship, while 8 of 10 shows a negative association. Thus, the hypothesized positive association is rejected, and the opposite, negative association is supported. The average $R^2$ value for negative associations is larger than for any other supported association; thus, this association is ranked first. Method C, which involves a full dataset STRAPP analysis can only be applied to species-level traits, and therefore cannot be applied to species richness. Figure 3 illustrates the negative and positive relationships of BAMM tip rates with tip-branch duration and body size, respectively, to which STRAPP analyses could be applied (Table 1C).

Finally, we assessed the role of an alternative habitat scheme upon rates of phenotypic evolution, to check if lacustrine environments elevate rates of phenotypic evolution as they do for speciation rates (Miller, 2021). We confirm this to be true; exclusively lacustrine taxa possess the highest mean and median rates, followed by

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

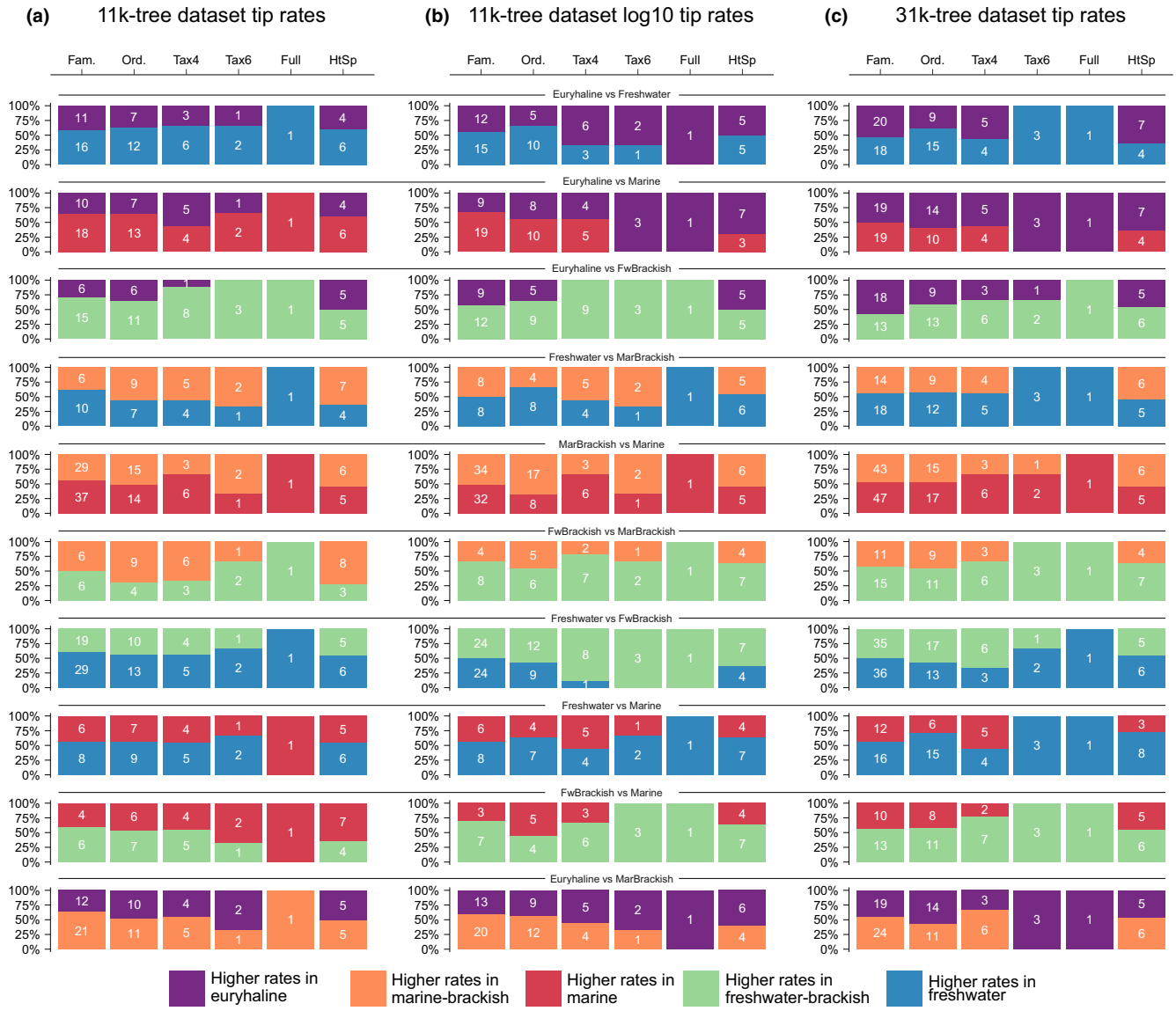


FIGURE 2 The percentage of clades where the average phenotypic rate in one habitat is larger than a second habitat to which it is being compared. Each row depicts comparison of two habitats, and white numbers capture how many groupings supported higher rates for a specific habitat. For example, row 1 column 1 in (a) shows that of the 27 fish families containing both euryhaline and freshwater species, the freshwater species showed higher rates of body size evolution in 59% of these families (i.e. 16 of 27). Comparisons are made between every unique pair of habitats (from five habitat types) across 10 scales of observation (6 shown, Supplementary Appendices 1–4 show results for all 10 scales using all examined rate metrics). The panels correspond to comparisons of (a) phenotypic rate upon the 11k-tree dataset; (b) log10 phenotypic rate upon the 11k-tree dataset and (c) log10 phenotypic rate upon the 31k-tree dataset. Presentation of logged and untransformed rate data shows how this decision impacts inferred patterns; firm conclusions are only drawn when all metrics agree. Taxonomic scale definitions are provided in methods. Fam. = Family, Ord. = Order, and HtSp = evolutionary hotspots.

simultaneously lacustrine + riverine taxa, followed by taxa in three habitats with comparable averages (diadromous taxa that migrate between saltwater and freshwater, exclusively marine, and exclusively riverine; Figure 4, Supplementary Appendix 11). Lacustrine taxa possess statistically higher rates than marine and riverine taxa (STRAPP; Supplementary Appendix 11). Furthermore, simultaneously lacustrine + riverine taxa possess statistically higher rates than exclusively riverine taxa (log10 rates phylogenetic ANOVA and STRAPP; Supplementary Appendix 11).

## 4 | DISCUSSION

### 4.1 | Mostly limited role for salinity habitat in driving rate differences

The effects of salinity upon rates of body size evolution have typically been explored in family-level analyses with variable methodologies and mostly comparing marine and freshwater settings. Results have varied, showing: (1) higher rates in freshwater species, specifically,

14680238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

**TABLE 1** Three hypothesized associations between rates of body size evolution and predictor variables, ranked from 1 (highest support) to 3 (least support) after considering results from three methods designed to assess the strength of these associations.

| **Approach A: Alignment of discrete outcomes**<br>Performed using 125 habitat comparisons at the order level.<br>Supplementary Appendix 5 shows where each hypothesized association, and Supplementary Appendix 6 shows % summaries of the order level comparisons. | **Approach B: Continuous relationship**<br>Assessed with regressions for 10 sets of pairwise habitat comparisons at order level.<br>See Supplementary Appendices 7–9 to view each regression, and Supplementary Appendix 10 for statistical summaries. | **Approach C: Continuous relationship**<br>Assessed with STRAPP using species-specific values. |
|---|---|---|
| 1. Testing the hypothesized positive association between **phenotypic rates and species richness**.<br>May expect, on average, that a group with more species has experienced higher speciation rates, and thus, would also possess higher phenotypic rates (given their previously established correlation in fishes). **Positive association not supported. Instead, a negative association has *moderate support*.** | | |
| Only 48/125 (38.4%) of comparisons support a positive association.<br>Positive association is particularly weak when comparing the specific habitats, where only 2/10 (20%) of Freshwater versus Marine–brackish comparisons, and 3/15 (20) Euryhaline versus Marine–brackish support a positive association. | 2/10 regressions support a positive association.<br>The two regressions have a mean $R^2 = 0.164$ and mean $p = 0.228$<br>**Instead, 8/10 regressions support negative association.** These eight regressions have a mean $R^2 = 0.174$ and mean $p = 0.326$ | Not applicable for method C, as species richness is a property of a group, not of species. |
| 2. Testing the hypothesized negative association between **phenotypic rates and branch duration**.<br>Expected given this relationship can be widely observed. ***Moderate support*.** | | |
| 75/125 (60%) of comparisons support a negative association.<br>Negative association is particularly strong when comparing specific comparisons, where 9/12 (75%) of Euryhaline versus Freshwater–brackish comparisons, and 14/19 (73.7%) of Marine–brackish versus Marine comparisons support a neg. association. | 8/10 regressions support a negative association. These eight regressions have a mean $R^2 = 0.07$, mean $p = 0.558$ | branch length log10 ~ size rate ($S = -0.361$, $p = 0$) |
| 3. Testing the hypothesized negative association between **phenotypic rates** and **size**.<br>Reasonable to hypothesize that, owing to the larger carrying capacity at lower trophic levels, smaller taxa may have a larger propensity for speciation than larger taxa. **No support for a negative association from approaches A and B, yet a *significant positive association* with approach C.** | | |
| 63/125 (50.4%) support a negative association.<br>The negative association is particularly poorly supported for Freshwater–brackish versus Marine comparisons, where support only occurs in 2/8 (25%) comparisons. | 6/10 regressions support a negative association. These six regressions have a mean $R^2 = 0.043$, mean $p = 0.676$ | Size log 10 ~ beta log10 ($S = 0.21$, $p = 0.002$) |

within pufferfishes (Tetraodontiformes; Santini et al., 2013), grunters (Terapontidae; Davis et al., 2014) and Apogonidae and Gobiidae + Gobionellidae (Thacker, 2014); (2) higher rates in marine sea catfishes (Ariidae; Betancur-R et al., 2012) and Upper Jurassic–end Palaeocene actinopterygian fishes (Guinot & Cavin, 2018) and (3) no clear evidence for salinity rate differences in needlefishes (Belonidae; Kolmann et al., 2020). Our study helps to contextualize these findings by repeatedly testing for rate differences among five salinity habitats for all groupings possible at 10 phylogenetic scales, while also permitting a reader to compare our results, using several metrics, to clade-level results of past and future studies (e.g. our Tetraodontidae and Belonidae results are in Supplementary Appendices 1–4).

Analyses at the full-dataset scale only recover one significant rate difference with one dataset and phylogenetic method: higher size rates in freshwater–brackish taxa versus marine in the 31k-tree dataset with the compare.rates function (Supplementary Appendices 3 and 4). In 9/10 pairwise salinity comparisons, no habitat displays consistently higher mean rates than another habitat across phylogenetic scales (i.e. present in most clades examined within most phylogenetic scales using most rate metrics; Figure 2 and Supplementary Appendices 1–4). This suggests that, unlike patterns of absolute body size differences between these same salinity settings, which are consistent and clear across scales and dataset types (Clarke, 2021), rate differences by salinity are mostly clade- and scale dependent. Therefore, despite classic literature characterizing freshwaters as slow-evolving environments producing living fossils (Darwin, 1859, 1877; Darwin & Seward, 1903), and contemporary efforts highlighting freshwaters as dynamic, high-paced environments for evolution due to fragmentation (Grosberg et al., 2012; May & Godfrey, 1994; Tedesco et al., 2017), neither marine nor freshwater taxa show higher mean rates than each other consistently across most scales (row 8 in both Figure 2 and Supplementary Appendices 1–4), consistent with arguments that both environments share important ecological opportunities (Friedman et al., 2022).

Based on the 11k-tree dataset, it can be argued that freshwater taxa more commonly possess higher rates at lower scales (e.g. family, order), and that marine taxa more commonly show higher rates at the full-dataset scale (Supplementary Appendices 1 and 2). This interpretation is consistent with our suggestion in the introduction

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

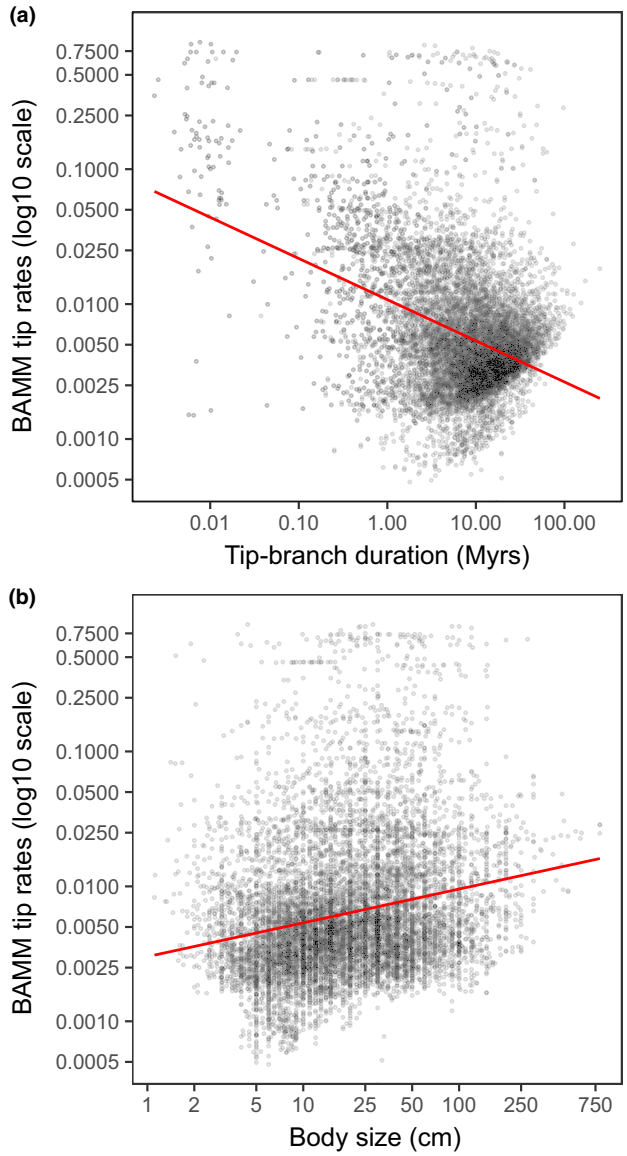


**FIGURE 3** Scatter plots of BAMM tip rates for body size evolution on a log10 scale as a response variable to (a) tip-branch duration and (b) body size. Regression lines are for illustrative purposes, more appropriate statistical outputs derived from STRAPP are reported in Table 1C. Tip rates represent the Brownian rate parameter with units of $\log(cm)^2/myr$.

that the greater morphological disparity of marine species (Friedman et al., 2022) could be underpinned by a higher mean rate at the whole-analysis scale for marine species, while the lower phylogenetic signal of freshwater lineages relative to marine, indicative of freshwater clades repeatedly re-evolving common morphologies (Friedman et al., 2022), could be underpinned by higher mean freshwater rates at lower taxonomic scales. The less robust, but more representative, 31k-supertree datasets increase the proportion of groups in which freshwater taxa possess higher rates than marine relatives at several scales (Figure 2c, Supplementary Appendices 3 and 4). Although we document a bias that elevates phenotypic rates in 31k-supertree datasets versus 11k-tree datasets (Figure 1), it cannot easily explain elevated freshwater rates relative to marine, as similar numbers of species from both habitats were added via supertree methods. However, it is possible that phylogenetic quality for supertree-added freshwater taxa is lower than for marine taxa, rendering the inflation artefactual. We therefore view the 31k-tree results with both interest and caution and await better-resolved phylogenies to determine whether higher freshwater rates in supertrees are artefactual, or are instead real, delivering an important high-rate freshwater signal that molecular trees currently miss. Together, the above findings resemble those from broad-scale comparisons of fish speciation rates by salinity (Miller, 2021; Rabosky, 2020) as follows: (1) rate differences between marine and freshwater rates can be subtle, and size rates by comparison are even more subtle, given the scarcity of significant differences recovered, whereas some significant speciation rate differences were found previously; (2) average rate differences between marine and freshwater, as recovered using a full dataset, can be driven by specific clades (e.g. higher speciation rates in freshwater fishes driven by Cichliformes in previous studies), albeit precisely how speciation rates differ across all the scales has currently not been documented in the manner we have here for phenotypic rates.

## 4.2 | Higher rates in freshwater–brackish species

The inclusion of lesser-studied euryhaline, freshwater–brackish and marine–brackish species was crucial to reveal the most consistent rate difference between any two habitats recovered in the study: in a majority of clades analysed for most taxonomic scales, and for all four metric types (and in the 31k-tree dataset), freshwater–brackish taxa possess higher rates versus their euryhaline relatives (row 3 in Figure 2). Thus, for this specific subset of brackish taxa at least, our broad-scale survey contrasts with studies finding low rates in brackish species (Kirchhoff et al., 2017; Santini et al., 2013). Although the result aligns with the prediction that smaller species could possess higher rates than larger species (freshwater–brackish species are on average smaller than euryhaline species; Clarke, 2021), this is not a compelling explanation, given we recovered the opposite, positive relationship between size and rates (Figure 3b). Elevated freshwater–brackish rates may be attributable to some of the factors initially hypothesized to elevate freshwater fish rates, such as fragmentation driving smaller population sizes, reproductive isolation and local adaptation (Tedesco et al., 2017), the potential for environmental variability or the high productivity of some brackish environments (Seehausen & Wagner, 2014), but higher resolution data are required to rigorously test their importance to freshwater-brackish species. Clarke (2021) estimated that freshwater–brackish settings receive an average of 362 transitions from freshwater (where species are the smallest on average) and a combined average of 175 transitions from euryhaline and marine–brackish habitats (where species are jointly the largest on average). Elevated freshwater–brackish rates may, therefore, occur as species arriving from opposite ends of the size spectrum rapidly evolve towards the medium body size optimum of

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

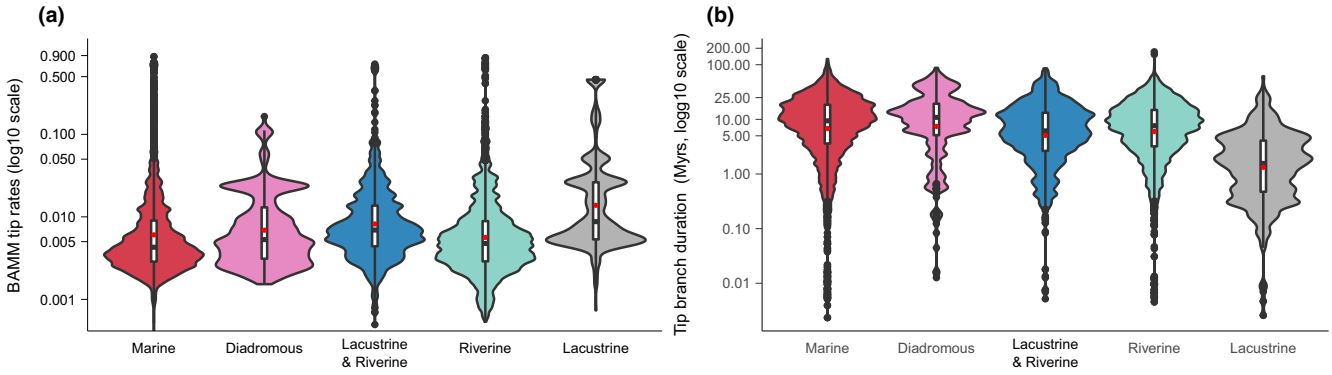


**FIGURE 4** Distributions of (a) phenotypic log10 tip rates, and (b) log10 tip-branch durations, for taxa in the alternative habitat categories of Miller (2021). Tip rates represent the Brownian rate parameter with units of log(cm)$^2$/myr.

freshwater–brackish taxa (Clarke, 2021), consistent with the finding that large amounts of size change occur when fishes transition into brackish/mixed settings (Guinot & Cavin, 2018). Furthermore, because the number of transitions into freshwater–brackish is high relative to both total freshwater–brackish species richness and the number of outward transitions (averages of 557 in, and 369 out; Clarke, 2021), perhaps lineages in neighbouring habitats already experiencing elevated rates of evolution (e.g. speciation and size) are those most likely to transition into freshwater–brackish, increasing the average rate of freshwater–brackish species. By contrast, euryhaline taxa, the strongest example of species to consistently show lower rates than freshwater-brackish across scales, loses more lineages than it gains (535 in, 700 out; Clarke, 2021), and so may frequently lose any lineages exhibiting high evolutionary rates to other environments. Despite higher rates in freshwater–brackish taxa versus euryhaline relatives being the most consistent result in our study, it is notable that this pattern is often weak or absent within "evolutionary hotspot" clades (HtSp column in Figure 2 and Supplementary Appendices 1–4). This highlights how clades that explore many salinity habitats (i.e. evolutionary hotspot clades) appear prone to showing atypical results (Clarke, 2021).

## 4.3 | Determining the relative importance of additional drivers of size rate variation

Given the limited ability for salinity to predict differences in size rates, we evaluated alternative drivers with three methods (Table 1). A reader can even view which drivers are plausibly active for up to 1056 comparisons made with the 11k-tree dataset in Supplementary Appendix 5. Taken together, the best-supported association is the negative relationship between species richness and size rates. We hypothesized a positive relationship based upon the known association between phenotypic rates and speciation rates (Rabosky et al., 2013) combined with an expectation that more species-rich groups (especially in our within-order comparisons, where smaller differences in branch duration can accrue) should generally be underpinned by higher speciation rates. However, support for a positive association between rates and species richness was seen in just ~38% of comparisons and only 2/10 regression analyses (Table 1A,B). Within our 125 order-level comparisons, it is rare for any habitat to display both high mean species richness and mean size rates simultaneously relative to a comparator group (i.e. if they existed, they would plot towards the outer corners of the white quadrants in Supplementary Appendix 7). Nevertheless, seven comparisons notably combine moderately high size rates with moderately high species richness, including marine Perciformes (vs. freshwater, marine–brackish and euryhaline relatives), freshwater–brackish Cyprinodontiformes (vs. euryhaline), euryhaline Clupeiformes (vs. freshwater–brackish), freshwater Siluriformes (vs. marine–brackish) and freshwater Characiformes (vs. freshwater–brackish). These seven outcomes may indicate where diversity-dependent mechanisms (i.e. where speciation rate decreases as the number of species increases; Rabosky, 2013; Rineau et al., 2022) are either absent, or simply do not impede higher phenotypic rates, highlighting them as good candidates for further study on this question.

Beyond these seven exemplars, most comparisons (~62%) show that the habitat with the higher mean size rates possesses lower species richness, and many display a substantial degree of mismatch, explaining why 8/10 regressions report negative associations (Table 1B, Supplementary Appendix 7). The absolute largest mismatch observed (i.e. combining higher size rates with lower richness relative to their compartor group) is seen in marine–brackish Cyprinodontiformes (vs. freshwater), followed by a host of substantial mismatches, including freshwater Tetraodontiformes (vs. marine), marine–brackish Cyprinodontiformes (vs. freshwater–brackish), marine–brackish Labriformes (vs. marine), euryhaline Chaetodontiformes (vs. marine–brackish), freshwater–brackish Perciformes (vs. freshwater) and numerous others (see points falling within central regions of grey quadrants in Supplementary Appendix 7). In all comparisons showing a mismatch, it is, therefore, plausible that diversity-dependent factors act to suppress phenotypic rates and/or ecological opportunity in the more species-rich groupings, and so we flag these groups for future study. Beyond these strong exemplars, the high prevalence of negative associations suggests that these processes may be commonplace in fishes.

The second strongest association is the negative relationship between size rates with branch duration (Table 1). The negative

14682238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

time scaling of evolutionary rates—where observed rates decrease as the time periods over which they are measured increase—appears to be a pervasive feature in evolutionary biology, with explanations ranging from incorrect model assumptions or artefacts as a result of estimation errors and/or sampling bias, to acceptance that the pattern is real (Harmon et al., 2021). Our study, therefore, confirms the presence of this phenomenon in the half of vertebrate diversity represented by fishes (Figure 3a). However, substantial rate variation occurs around the proportion explained by branch duration. Thus, while it is generally true that a very long branch will possess a lower rate than a very short branch, if the branches being compared are not orders of magnitude different in duration, then the shorter branch might not show higher rates than the longer one. This explains why STRAPP (which considers the whole dataset) shows a strong, significant negative relationship, while this negative association is weak with approaches A and B (where 60% of binary comparisons show negative associations, and the negative regressions average a small $R^2$ of 0.07 respectively; Table 1A,B); this is because approaches A and B compare habitats within orders that generally do not differ by large amounts in their average tip-branch durations. When moderate to large differences in tip-branch durations do emerge (i.e. points that plot further away from 0 on the x-axis in Supplementary Appendix 8), most support a negative association (i.e. they plot within grey quadrants), which produces negative relationship regressions. Notably, the shorter tip-branch durations of lacustrine taxa habitats appear to underpin their higher phenotypic rates relative to other habitats (Figure 4). In rare cases, habitats show both substantially longer average tip-branch durations and higher rates than their relatives from another habitat, including marine–brackish Cyprinodontiformes (vs. euryhaline) and euryhaline Chaetodontiformes (vs. marine) (Supplementary Appendix 8).

Although we had predicted that smaller taxa would possess higher rates of size evolution, we instead found a significant positive relationship between body size and rate using STRAPP on the full dataset (Table 1C, S = 0.21, $p = 0.002$). However, results were evenly split between positive and negative associations with approaches A and B (Table 1A,B). The failure of approaches A and B to clearly support a positive relationship can be explained by the low Spearman's value (0.21) in approach C, revealing that substantial variation in rate is not explained by size (Figure 3b). As such, the differences in mean size between any comparisons in approaches in A and B would regularly need to be very large to frequently detect a positive association, which is unlikely for within-order comparisons.

A positive association between size and size rates, where rates of size evolution increase as absolute body size increases, agrees with equivalent findings in both mammals (Monroe & Bokma, 2009) and perches (Arbour & Stanchak, 2021). Yet, closer examination reveals key features. First, the very highest rates occur in the middle of the size distribution (Figure 3b), although this may occur because most species reside in this region, and so there are more opportunities for higher rates to arise by chance. Second, the distribution of rates appears to shift suddenly to higher rates in both the very largest and very smallest taxa (Figure 3b). Specifically, the very lowest rates occur in fishes between 5 and 10 cm long, but below 5 cm, rates increase, suddenly forming a distribution of low-medium rates, and then, at sizes below 2 cm, to rates close to 0.01 and above. Similarly, at the very largest sizes, only rates of around ~0.0025 occur. Finding higher size rates at body size extremes resembles the finding of higher size rates at trophic extremes in reef fishes (Borstein et al., 2019). Thus, several nuanced relationships can occur between size and size rates even within the context of a broad positive association.

Finally, we considered the impact of lakes on phenotypic rates by implementing the alternative habitat scheme of Miller (2021), and found significantly higher rates in lacustrine habitats relative to marine and riverine taxa (Supplementary Appendix 11), confirming that patterns seen for speciation rate (Miller, 2021) are matched by size rates. Importantly, elevated rates in lakes are not an isolated phenomenon restricted to cichlids (Burress & Muñoz, 2023), and it is observed in a wide variety of orders (Supplementary Appendix 12): most notably for Cyprinodontiformes, Clupeiformes, Siluriformes, Cypriniformes, Osmeriformes, Beloniformes and Atheriniformes, though it is absent for Osteoglossiformes, Perciformes and Synbranchiformes. Elevated rates in lakes are consistent with evolutionary theory, as lake radiations are commonly cited as providing ecological opportunity for adaptive radiations of species, characterized by rapid speciation and phenotypic differentiation (Schluter, 2000; Simpson, 1953). Furthermore, we expect phenotypic rates to be enhanced by the greater depth profile of lakes, presenting greater habitat variety (Lucek et al., 2016; Recknagel et al., 2017), the shorter tip-branch durations of lacustrine species (Figure 4b), and as a result of the longer food chains in lakes due to phytoplankton-based food webs (Potapov et al., 2019), which should produce greater body size variety.

## 5 | Conclusion

Rates of body size evolution rarely show consistent differences between salinity habitats in a way that is maintained for most clades examined at most phylogenetic scales. Our consistent methodology applied to all comparisons contextualizes previous mostly family- or order-focused studies comparing marine and freshwater rates, where approximately half support higher rates in marine species (Betancur-R et al., 2012; Guinot & Cavin, 2018) and half support higher rates in freshwater species (Davis et al., 2014; Santini et al., 2013; Thacker, 2014). While this conflicting impression from a small collection of studies could easily have been artefactual (e.g. driven by clade choice or methodology), we reveal it does not hugely depart from our results showing an approximately even split regarding whether marine or freshwater clades have higher rates. However, marine versus freshwater patterns can slightly deviate from this 50/50 pattern with scale, with freshwater rates more likely to exceed those of marine relatives at lower scales, and the opposite at the largest scales, which is potentially associated with the lower phylogenetic signal of freshwater phenotypes relative to marine ones.

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Separately, freshwater–brackish taxa do possess consistently higher rates compared with euryhaline taxa at most scales examined. Tests of additional drivers of rate variation reveal that low species richness and short tip-branch durations are associated with higher rates of size evolution, with more subtle evidence of higher rates associated with greater absolute body size. Finally, we found significantly elevated rates of size evolution within lacustrine species relative to all other habitats, and species inhabiting both rivers and lakes relative to exclusively riverine species. Together, our analyses reveal the rate patterns that underpin global patterns of body size for fishes, identifying both factors that play a limited role (i.e. salinity) and those that explain considerable amounts of rate variation across half of vertebrate diversity.

## ACKNOWLEDGEMENTS

J.T.C. thanks Sebastian Höhna, Bjørn Kopperud, Toomas Tammaru and Marcin Piwczyński for useful discussion and support. J.T.C was supported by the Alexander von Humboldt Foundation, iDiv (funded by the German Research Foundation; DFG–FZT 118, 202548816), and the Polish National Agency for Academic Exchange (NAWA; PPN/ULM/2019/1/00248/U/00001). R.B.D was supported by the Estonian Research Council (grant PRG741 to Toomas Tammaru). Open Access funding enabled and organized by Projekt DEAL.

## CONFLICT OF INTEREST STATEMENT

None.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supplementary Material of this article.

## ORCID

*John T. Clarke* https://orcid.org/0000-0003-1321-2988
*Robert B. Davis* https://orcid.org/0000-0002-0104-0747

## REFERENCES

Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, *4*, 393–399.

Arbour, J. H., & Stanchak, K. E. (2021). The little fishes that could: Smaller fishes demonstrate slow body size evolution but faster speciation in the family Percidae. *Biological Journal of the Linnean Society*, *134*, 851–866.

Betancur-R, R., Ortí, G., Stein, A. M., Marceniuk, A. P., & Alexander Pyron, R. (2012). Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. *Ecology Letters*, *15*, 822–830.

Blackburn, T. M., & Gaston, K. J. (2002). Scale in macroecology. *Global Ecology and Biogeography*, *11*, 185–189.

Borstein, S. R., Fordyce, J. A., O'Meara, B. C., Wainwright, P. C., & McGee, M. D. (2019). Reef fish functional traits evolve fastest at trophic extremes. *Nature Ecology & Evolution*, *3*, 191–199.

Burress, E. D., & Muñoz, M. M. (2023). Phenotypic rate and state are decoupled in response to river-to-lake transitions in cichlid fishes. *Evolution*, *77*, 2365–2377.

Clarke, J. T. (2021). Evidence for general size-by-habitat rules in actinopterygian fishes across nine scales of observation. *Ecology Letters*, *24*, 1569–1581.

Collyer, M. L., & Adams, D. C. (2018). RRPP: An r package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*, *9*, 1772–1779.

Cooney, C. R., & Thomas, G. H. (2020). Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, *5*, 101–110.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray.

Darwin, C. (1877). *Descent of man, and selection in relation to sex. Revised and augmented 2nd edition, including an essay by T. H. Huxley*. John Murray.

Darwin, F., & Seward, A. C. (1903). *More letters of Charles Darwin: A record of his work in a series of hitherto unpublished letters*. D. Appleton.

Davis, A. M., Unmack, P. J., Pusey, B. J., Pearson, R. G., & Morgan, D. L. (2014). Effects of an adaptive zone shift on morphological and ecological diversification in terapontid fishes. *Evolutionary Ecology*, *28*, 205–227.

Finlay, B. J., Thomas, J. A., McGavin, G. C., Fenchel, T., & Clarke, R. T. (2006). Self-similar patterns of nature: Insect diversity at local to global scales. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1935–1941.

Foody, G. M. (2004). Spatial nonstationarity and scale-dependency in the relationship between species richness and environmental determinants for the sub-Saharan endemic avifauna. *Global Ecology and Biogeography*, *13*, 315–320.

Friedman, S. T., Collyer, M. L., Price, S. A., & Wainwright, P. C. (2022). Divergent processes drive parallel evolution in marine and freshwater fishes. *Systematic Biology*, *71*, 1319–1330.

Froese, R., & Pauly, D. (Eds.). (2000). *FishBase 2000: Concepts, designs and data sources*. WorldFish.

Grosberg, R. K., Vermeij, G. J., & Wainwright, P. C. (2012). Biodiversity in water and on land. *Current Biology*, *22*, R900–R903.

Guinot, G., & Cavin, L. (2018). Body size evolution and habitat colonization across 100 million years (Late Jurassic–Paleocene) of the actinopterygian evolutionary history. *Fish and Fisheries*, *19*, 577–597.

Harmon, L. J., Pennell, M. W., Henao-Diaz, L. F., Rolland, J., Sipley, B. N., & Uyeda, J. C. (2021). Causes and consequences of apparent Timescaling across all estimated evolutionary rates. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 587–609.

Igea, J., Miller, E. F., Papadopulos, A. S. T., & Tanentzap, A. J. (2017). Seed size and its rate of evolution correlate with species diversification across angiosperms. *PLoS Biology*, *15*, e2002792.

Kirchhoff, K. N., Hauffe, T., Stelbrink, B., Albrecht, C., & Wilke, T. (2017). Evolutionary bottlenecks in brackish water habitats drive the colonization of fresh water by stingrays. *Journal of Evolutionary Biology*, *30*, 1576–1591.

Kolmann, M. A., Burns, M. D., Ng, J. Y. K., Lovejoy, N. R., & Bloom, D. D. (2020). Habitat transitions alter the adaptive landscape and shape phenotypic evolution in needlefishes (Belonidae). *Ecology and Evolution*, *10*, 3769–3783.

Lee, C. E., & Bell, M. A. (1999). Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology & Evolution*, *14*, 284–288.

Losos, J. B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist*, *175*, 623–639.

Lucek, K., Kristjánsson, B. K., Skúlason, S., & Seehausen, O. (2016). Ecosystem size matters: The dimensionality of intralacustrine diversification in Icelandic stickleback is predicted by lake size. *Ecology and Evolution*, *6*, 5256–5272.

May, R. M., & Godfrey, J. (1994). Biological diversity: Differences between land and sea [and discussion]. *Philosophical Transactions: Biological Sciences*, *343*, 105–111.

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

McClain, C. R., & Nekola, J. C. (2008). The role of local-scale processes on terrestrial and deep-sea gastropod body size distributions across multiple scales. *Evolutionary Ecology Research*, *10*, 129–146.
Miller, E. C. (2021). Comparing diversification rates in lakes, rivers, and the sea. *Evolution*, *75*, 2055–2073.
Mitterboeck, T. F., Chen, A. Y., Zaheer, O. A., Ma, E. Y. T., & Adamowicz, S. J. (2016). Do saline taxa evolve faster? Comparing relative rates of molecular evolution between freshwater and marine eukaryotes. *Evolution*, *70*, 1960–1978.
Monroe, M. J., & Bokma, F. (2009). Do speciation rates drive rates of body size evolution in mammals? *The American Naturalist*, *174*, 912–918.
Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.
Potapov, A. M., Brose, U., Scheu, S., & Tiunov, A. V. (2019). Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist*, *194*, 823–839.
Puebla, O. (2009). Ecological speciation in marine v. freshwater fishes. *Journal of Fish Biology*, *75*, 960–996.
Rabosky, D. L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 481–502.
Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth–death polytomy resolvers for downstream comparative analyses. *Evolution*, *69*, 3207–3216.
Rabosky, D. L. (2020). Speciation rate and the diversity of fishes in freshwaters and the oceans. *Journal of Biogeography*, *47*, 1207–1217.
Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *559*, 392–395.
Rabosky, D. L., Grundler, M., Anderson, C., Title, P., Shi, J. J., Brown, J. W., Huang, H., & Larson, J. G. (2014). BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, *5*, 701–707.
Rabosky, D. L., & Huang, H. (2016). A robust semi-parametric test for detecting trait-dependent diversification. *Systematic Biology*, *65*, 181–193.
Rabosky, D. L., Santini, F., Eastman, J., Smith, S. A., Sidlauskas, B., Chang, J., & Alfaro, M. E. (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*, *4*, 1958.
Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*, 224–239.
Recknagel, H., Hooker, O. E., Adams, C. E., & Elmer, K. R. (2017). Ecosystem size predicts eco-morphological variability in a postglacial diversification. *Ecology and Evolution*, *7*, 5560–5570.
Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.
Rineau, V., Smyčka, J., & Storch, D. (2022). Diversity dependence is a ubiquitous phenomenon across Phanerozoic oceans. *Science Advances*, *8*, eadd9620.
Santini, F., Nguyen, M. T. T., Sorenson, L., Waltzek, T. B., Lynch Alfaro, J. W., Eastman, J. M., & Alfaro, M. E. (2013). Do habitat shifts drive diversification in teleost fishes? An example from the pufferfishes (Tetraodontidae). *Journal of Evolutionary Biology*, *26*, 1003–1018.
Schluter, D. (2000). Ecological character displacement in adaptive radiation. *The American Naturalist*, *156*, S4–S16.
Seehausen, O., & Wagner, C. E. (2014). Speciation in freshwater fishes. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 621–651.
Simpson, G. G. (1953). *The major features of evolution*. Columbia University Press.
Slater, G. J., & Friscia, A. R. (2019). Hierarchy in adaptive radiation: A case study using the Carnivora (Mammalia). *Evolution*, *73*, 524–539.
Tedesco, P. A., Paradis, E., Lévêque, C., & Hugueny, B. (2017). Explaining global-scale diversification patterns in actinopterygian fishes. *Journal of Biogeography*, *44*, 773–783.
Thacker, C. E. (2014). Species and shape diversification are inversely correlated among gobies and cardinalfishes (Teleostei: Gobiiformes). *Organisms Diversity & Evolution*, *14*, 419–436.

## BIOSKETCH

John T. Clarke is an evolutionary biologist and macroecologist interested in the application of phylogenetic comparative methods to large datasets spanning living and fossil fishes, plants and insects, in order to test for the presence or absence of general patterns concerning the evolution and distribution of morphological traits and diversification rates across the Tree of Life. Robert B. Davis is an evolutionary biologist and ecologist who is interested in the use of phylogenies to answer evolutionary and ecological questions. While mainly using comparative methods on insects, his interests span beyond this to other uses of phylogenies and other taxa.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Clarke, J. T., & Davis, R. B. (2024). Salinity plays a limited role in determining rates of size evolution in fishes globally across multiple scales. *Global Ecology and Biogeography*, *33*, e13883. https://doi.org/10.1111/geb.13883

14668238, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13883, Wiley Online Library on [25/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License